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Stationary solutions of linear stochastic delay differential equations: Applications to biological systems

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Recently, Küchler and Mensch [Stochastics Stochastics Rep. **40**, 23 (1992)] derived exact stationary probability densities for linear stochastic delay differential equations. This paper presents an alternative derivation of these solutions by means of the Fokker-Planck approach introduced by Guillouzic [Phys. Rev. E **59**, 3970 (1999); **61**, 4906 (2000)]. Applications of this approach, which is argued to have greater generality, are discussed in the context of stochastic models for population growth and tracking movements.

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I. INTRODUCTION

Recently, there has been a growing interest in the effects of noise on dynamical systems with delays. In biological systems, both noise and delays are inevitable. Noise is immanent in any open system involving up-take and dissipation of energy. Delays usually arise due to finite information transmission times. In this context, delayed visual feedback systems [1–9], stochastic resonance and oscillator ensembles with delayed interactions [10–14], synchronization of human movements [15], field theoretical models of brain activity [16–23], and disturbed speech control due to delayed auditory feedback (the so-called Lee effect; see Refs. [6,24] and references therein) have been studied. Furthermore, as an alternative to motor control models without delays [25–29], stochastic models with delays have been proposed to describe postural sway [30–34].

Despite a potentially wide range of applications for stochastic processes with delays, the explicit structures of their stationary probability densities have hardly been studied. Using stochastic delay differential equations (SDDE's), Mackey and Nechaeva [35] and Küchler and Mensch [36] succeeded in identifying parameter regimes in which stationary solutions exist. Küchler and Mensch also obtained stationary solutions for linear SDDE's with finite delays, while Guillouzic *et al.* derived stationary solutions for nonlinear SDDE's in the limit of very small delays using a Fokker-Planck approach [37,38]. In the present paper, the findings of Küchler and Mensch and Guillouzic *et al.* will be combined in order to derive stationary probability densities for linear SDDE's with finite delays by means of the Fokker-Planck approach.

In general, the Fokker-Planck approach to stochastic processes is superior to the approach via stochastic differential equations, because only in the former case can stationary probability densities for nonlinear drift forces be obtained. For this reason, a theory of time-continuous stochastic processes with delays should preferably be based on the theory of Fokker-Planck equations. In order to develop such a theory of Fokker-Planck equations with delays, a first but essential step is to discuss the linear case, in which stationary solutions can be compared with those derived from the corresponding linear SDDE's. The first part of this paper, Sec. II, will be devoted to this subject.

The second part of this paper, Sec. III, is concerned with applications of the results obtained in Sec. II. In particular, two models will be discussed that are well established in the literature: a model for population growth, and a deterministic model for rhythmic tracking movements under delayed visual feedback. The former model will be extended to cope with fluctuations and delays in the dynamics. The latter model will be extended to account for motor variability. In Sec. III we will also show how to analyze nonlinear SDDE's by means of the stationary probability density derived for the linear case.

II. STATIONARY SOLUTIONS OF LINEAR SDDE'S

A. Derivation of stationary probability densities

We consider the evolution of a dimensionless random variable $\xi'(t')$ defined on the real line. Here t' denotes time measured in arbitrary units (denoted as TU'). Let $\Gamma'(t')$ denote a Langevin force with $\langle\Gamma'(t')\Gamma'(s')\rangle=\delta(t'-s')$, where $\langle\cdot\rangle$ is the ensemble average and $\delta(\cdot)$ is the delta distribution [39–41]. Furthermore, let $\tau'\geqslant 0$ denote the delay. We now assume that $\xi'(t')$ satisfies the SDDE

$$\frac{d}{dt'}\xi'(t')=-\gamma_1'\xi'(t')-\gamma_2'\xi'(t'-\tau')+\sqrt{Q'}\Gamma'(t') \tag{1}$$

for $t'\geqslant t_0'$, and $\xi'(t')=\Phi'(t')$ for $t'\in[t_0'-\tau',t_0']$. Here $\gamma_1'\geqslant 0$, $\gamma_2'>0$, and $Q'>0$ correspond to friction coefficients and the fluctuation strength, respectively. $\Phi'(t')$ describes the initial condition of the stochastic process in terms of a graph defined on $[t_0'-\tau',t_0']$. For the sake of convenience, we eliminate the fluctuation strength Q' by introducing new variables $t:=Q't'$, $\tau:=Q'\tau'$, $t_0:=Q't_0'$, $\xi(t):=\xi'(t/Q')$, $\gamma_1:=\gamma_1'/Q'$, $\gamma_2:=\gamma_2'/Q'$, $\Phi(t):=\Phi'(t/Q')$, and $\Gamma(t):=\Gamma'(t/Q')/\sqrt{Q'}$. Now time is measured in units $TU=TU'[Q']$, where $[Q']$ denotes the units in which the fluctuation strength is described. Then Eq. (1) can be transformed into

$$\frac{d}{dt}\xi(t)=-\gamma_1\xi(t)-\gamma_2\xi(t-\tau)+\Gamma(t) \tag{2}$$

for $t \geqslant t_0$ and $\xi(t)=\Phi(t)$ for $t\in[t_0-\tau,t_0]$. In addition, we have $\langle\Gamma(t)\Gamma(s)\rangle=\delta(t-s)$. Küchler and Mensch showed that for natural boundary conditions and $\gamma_2>\gamma_1\geqslant 0$ a stationary solution of Eq. (2) exists if and only if $0\leqslant\tau\sqrt{\gamma_2^2-\gamma_1^2}<\arccos(-\gamma_1/\gamma_2)\leqslant\pi/2$ [see Ref. [36] Eqs. (2.17) and (2.18)]. In particular, for $\gamma_1=0$ we have the condition $\gamma_2\tau\in[0,\pi/2)$. To exploit also the results obtained by Guillouzic *et al.* [37], we assume for the moment that the stochastic process [Eq. (2)] is subjected to reflecting boundaries at $\pm A$. In this case, the process described by Eq. (2) solves the delay Fokker-Planck equation

$$\begin{aligned}\frac{\partial}{\partial t}\mathcal{P}(x,t)&=-\frac{\partial}{\partial x}S^A(x,t)\\&:=\gamma_1\frac{\partial}{\partial x}x\mathcal{P}(x,t)+\gamma_2\frac{\partial}{\partial x}\mathcal{P}(x,t)\\&\quad\times\int_{-A}^{A}y\,\mathcal{P}(y,t-\tau|x,t)dy+\frac{1}{2}\frac{\partial^2}{\partial x^2}\mathcal{P}(x,t)\end{aligned}\tag{3}$$

for $t\geqslant t_0$, where $\mathcal{P}(x,t)$ denotes the process probability density, $S^A(x,t)$ is the probability current, and $\mathcal{P}(y,t-\tau|x,t)$ is a conditional probability density. Both $\mathcal{P}(x,t)$ and $\mathcal{P}(y,t-\tau|x,t)$ are subjected to the initial condition $\mathcal{P}(x,t)=\delta(x-\Phi(t))$ for $t\in[t_0-\tau,t_0]$. The stationary solution $\mathcal{P}_{\rm st}$ of Eq. (3) satisfies

$$\begin{aligned}&\gamma_1 x\mathcal{P}_{\rm st}^A(x)+\gamma_2\mathcal{P}_{\rm st}^A(x)\int_{-A}^{A}y\mathcal{P}_{\rm st}^A(y,t-\tau|x,t)dy+\frac{1}{2}\frac{\partial}{\partial x}\mathcal{P}_{\rm st}^A(x)\\&\quad=-S^A=\text{const}.\end{aligned}\tag{4}$$

We have not been able to solve Eq. (4) with respect to $\mathcal{P}_{\rm st}(x)$ for finite boundaries $\pm A$. However, as we will show below, a solution can be found in the limit $A\to\infty$. For this reason, we solve the SDDE (2) for natural boundary conditions (NBC's). To this end, we assume that if the stationary solution $\mathcal{P}_{\rm st}^{\rm NBC}$ of Eq. (2) exists, it can be derived as the distribution $\mathcal{P}_{\rm st}^A(x)$ in the limit $A\to\infty$. This implies that $\mathcal{P}_{\rm st}^{\rm NBC}(x)$ solves the integrodifferential equation

$$\begin{aligned}&\gamma_1\mathcal{P}_{\rm st}^{\rm NBC}(x)+\gamma_2\mathcal{P}_{\rm st}^{\rm NBC}(x)\int_{-\infty}^{\infty}y\,\mathcal{P}_{\rm st}^{\rm NBC}(y,t-\tau|x,t)dy\\&\quad+\frac{1}{2}\frac{\partial}{\partial x}\mathcal{P}_{\rm st}^{\rm NBC}(x)=-S^{\rm NBC}=0.\end{aligned}\tag{5}$$

Note that the stationary probability current $S^{\rm NBC}$ vanishes, because we have $\mathcal{P}_{\rm st}^{\rm NBC}(x\to\pm\infty)=0$ (a normalization condition).

Before solving Eq. (5) with respect to $\mathcal{P}_{\rm st}^{\rm NBC}(x)$, we would like to stress a fundamental property of Eq. (5), which will support the validity of our approach. Let us define the stationary $n{:}1$ autocorrelation $K_{\rm st}^{(n)}(\Delta t)$ of the random variable $\xi(t)$ for $n\geqslant 1$ by

$$\begin{aligned}K_{\rm st}^{(n)}(\Delta t)&:=\langle\xi^n(t)\xi(t-\Delta t)\rangle_{\rm st}\\&=\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}x^n y\,\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\Delta t)dx\,dy,\end{aligned}\tag{6}$$

where $\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\Delta t)$ is the joint probability density in the stationary case. Using the identity $\mathcal{P}_{\rm st}^{\rm NBC}(x)\mathcal{P}_{\rm st}^{\rm NBC}(y,t-\tau|x,t)=\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\tau)$ (also see Ref. [37], p. 3971), we can rewrite Eq. (5) as

$$\begin{aligned}&\gamma_2\int_{-\infty}^{\infty}y\,\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\tau)dy\\&\quad=-\gamma_1 x\mathcal{P}_{\rm st}^{\rm NBC}(x)-\frac{1}{2}\frac{\partial}{\partial x}\mathcal{P}_{\rm st}^{\rm NBC}(x).\end{aligned}\tag{7}$$

We now multiply the left and right hand sides of Eq. (7) by x^n, integrate with respect to x, and evaluate the right hand side obtained by partial integration. This gives us

$$\begin{aligned}K_{\rm st}^{(n)}(\Delta t=\tau)&=\frac{n}{2\gamma_2}\int_{-\infty}^{\infty}x^{n-1}\mathcal{P}_{\rm st}^{\rm NBC}(x)dx\\&\quad-\frac{\gamma_1}{\gamma_2}\int_{-\infty}^{\infty}x^{n+1}\mathcal{P}_{\rm st}^{\rm NBC}(x)dx\\&\overset{\gamma_1=0}{\Rightarrow}K_{\rm st}^{(1)}(\Delta t=\tau;\gamma_1=0)=\frac{1}{2\gamma_2}.\end{aligned}\tag{8}$$

Consequently, for $\gamma_1=0$, the stationary 1:1 autocorrelation $K_{\rm st}^{(1)}(\Delta t)$ for $\Delta t=\tau$ is reciprocal to twice the friction coefficient γ_2, irrespective of the delay length τ. This result was previously derived by Küchler and Mensch, who used an approach different from the Fokker-Planck approach presented here [71].

We now solve Eq. (5) with respect to $\mathcal{P}_{\rm st}^{\rm NBC}(x)$. To this end, we consider Eq. (5) in the form of Eq. (7) and—in line with the work of Küchler and Mensch, who showed that the stationary solution of the Eq. (2) is a Gaussian process [36]—we use the ansatz

$$\mathcal{P}_{\rm st}^{\rm NBC}(x)=\sqrt{\frac{\lambda(\tau)}{\pi}}\exp\{-\lambda(\tau)x^2\},\tag{9}$$

$$\mathcal{P}_{\rm st}^{\rm NBC}(x,t|y,t-\tau)=\sqrt{\frac{a(\tau)}{\pi}}\exp\{-a(\tau)[x-b(\tau)y]^2\},\tag{10}$$

$$\begin{aligned}&\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\tau)\\&\quad=\frac{\sqrt{a(\tau)\lambda(\tau)}}{\pi}\exp\{-a(\tau)[x-b(\tau)y]^2-\lambda(\tau)y^2\}.\end{aligned}\tag{11}$$

Note that this ansatz involves three coefficients λ, a, and b which, in general, depend on the delay τ. By substituting Eq. (9) into the right hand side of Eq. (7), and Eq. (11) into the left hand side of Eq. (7), and by carrying out the integration with respect to y, we obtain (see the Appendix)

$$\gamma_2 \frac{a^{3/2}b}{(ab^2+\lambda)^{3/2}} x \exp\left\{ -\frac{a\lambda}{ab^2+\lambda}x^2 \right\} = (\lambda-\gamma_1)x \exp\{-\lambda x^2\}. \tag{12}$$

Equation (12) is satisfied for all $x\in\mathbb{R}$ if the factors and exponents of both sides coincide. Consequently, we find the conditions

$$\gamma_2 \frac{a^{3/2}b}{(ab^2+\lambda)^{3/2}} = \lambda-\gamma_1 \quad \text{and} \quad ab^2+\lambda=a. \tag{13}$$

Using Eq. (13), we can express $a(\tau)$ and $b(\tau)$ in terms of $\lambda(\tau)$ and obtain

$$a(\tau)=\frac{\lambda(\tau)}{1-\left(\frac{\lambda(\tau)-\gamma_1}{\gamma_2}\right)^2} \quad \text{and} \quad b(\tau)=\frac{\lambda(\tau)-\gamma_1}{\gamma_2}. \tag{14}$$

According to Küchler and Mensch, for $\gamma_2>\gamma_1\geqslant 0$ the variance $\sigma^2(\tau)$ of the process given by Eq. (2) reads

$$\sigma^2(\tau)=\frac{\gamma_2 \sin(\sqrt{\gamma_2^2-\gamma_1^2}\tau)+\sqrt{\gamma_2^2-\gamma_1^2}}{2\sqrt{\gamma_2^2-\gamma_1^2}\cdot[\gamma_1+\gamma_2\cos(\sqrt{\gamma_2^2-\gamma_1^2}\tau)]} \tag{15}$$

with $0\leqslant\tau\sqrt{\gamma_2^2-\gamma_1^2}<\arccos(-\gamma_1/\gamma_2)\leqslant\pi$; see Ref. [36] Eq. 2.28. Note that for $\gamma_1>\gamma_2\geqslant 0$, and $\gamma_1=\gamma_2\geqslant 0$ equations similar to Eq. (15) can be derived. Since $\sigma^2(\tau)$ is related to $\lambda(\tau)$ by $\sigma^2(\tau)=1/2\lambda(\tau)$, we can therefore express $\lambda(\tau)$ as

$$\lambda(\tau)=\frac{\sqrt{\gamma_2^2-\gamma_1^2}\cdot[\gamma_1+\gamma_2\cos(\sqrt{\gamma_2^2-\gamma_1^2}\tau)]}{\gamma_2 \sin(\sqrt{\gamma_2^2-\gamma_1^2}\tau)+\sqrt{\gamma_2^2-\gamma_1^2}}. \tag{16}$$

Let us briefly discuss the results obtained so far. In the limit of a vanishing delay, that is, for $\tau\to 0$, we obtain $\lambda(0)=\gamma_1+\gamma_2$, $b(0)=1$, and $a\to\infty$. The corresponding stationary solution $\mathcal{P}_{\rm st}^{\rm NBC}(x)$ with $\lambda(0)=\gamma_1+\gamma_2$ coincides with the stationary probability density of an ordinary Ornstein-Uhlenbeck process. Furthermore, the conditional probability density [Eq. (10)] converges to a δ-distribution, that is, $\lim_{\tau\downarrow 0}\mathcal{P}_{\rm st}^{\rm NBC}(x,t|y,t-\tau)=\delta(x-y)$. Similarly, the joint probability density [Eq. (11)] converges like $\lim_{\tau\downarrow 0}\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\tau)=\delta(x-y)\mathcal{P}_{\rm st}^{NBC}(y)$. Consequently, Eq. (7) reduces to

$$(\gamma_1+\gamma_2)x\mathcal{P}_{\rm st}^{\rm NBC}(x)=-\frac{1}{2}\frac{\partial}{\partial x}\mathcal{P}_{\rm st}^{\rm NBC}(x), \tag{17}$$

which is a well-known expression in the theory of ordinary Ornstein-Uhlenbeck processes. For small delay τ and $\gamma_1=0$, we can expand $\lambda(\tau)$ given by Eq. (16) into a Taylor series, and thus reobtain the results obtained by Guillouzic *et al.* (Ref. [37] Eq. (31)). From Eq. (16) it follows that in the limit $\tau\uparrow\arccos(-\gamma_1/\gamma_2)/\sqrt{\gamma_2^2-\gamma_1^2}$ the coefficient $\lambda(\tau)$ vanishes. Consequently, the Gaussian distribution [Eq. (9)] converges to a uniform distribution.

In the previous derivation we assumed that Eq. (11) represents a stationary joint probability density. That is, $\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\tau)$ satisfies

$$\int_{-\infty}^{\infty}\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\tau)dx=\mathcal{P}_{\rm st}^{\rm NBC}(y) \quad \text{and}$$

$$\int_{-\infty}^{\infty}\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\tau)dy=\mathcal{P}_{\rm st}^{\rm NBC}(x), \tag{18}$$

where $\mathcal{P}_{\rm st}^{\rm NBC}(\cdot)$ is given by Eq. (9). The first relation can be immediately verified. The second relation, however, is only satisfied for $ab^2+\lambda=a$, as can be shown by detailed calculations similar to those carried out in the Appendix. Consequently, we again encounter the condition on the right hand side of Eq. (13). Using this condition, we can eliminate λ in Eq. (11), and obtain

$$\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\tau)=\frac{a(\tau)\sqrt{1-b^2(\tau)}}{\pi}\times\exp\{-a(\tau)[x^2+y^2-2b(\tau)xy]\}. \tag{19}$$

We now return to the calculation of the $n{:}1$ autocorrelation [Eq. (8)] for $\gamma_1=0$. Substituting Eq. (9) into Eq. (8), for $\gamma_1=0$ we obtain

$$K_{\rm st}^{(n)}(\tau;\gamma_1=0)=\begin{cases} 0 & \text{for } n \text{ even} \\ \dfrac{n[1\cdot 3\cdot 5\cdots(n-2)]}{\gamma_2 2^{(n+1)/2}\lambda(\tau)^{(n-1)/2}} & \text{for } n \text{ odd.}\end{cases} \tag{20}$$

In particular, we obtain

$$K_{\rm st}^{(3)}(\tau;\gamma_1=0)=\langle\xi^3(t)\xi(t-\tau)\rangle_{\rm st} = \frac{3}{2\,\gamma_2}\sigma^2(\tau) = \frac{3[1+\sin(\gamma_2\tau)]}{4\,\gamma_2^2\cos(\gamma_2\tau)}. \tag{21}$$

Using Eq. (11), we can also determine $n{:}m$ autocorrelations $C^{(n:m)}(\Delta t)$ for $\Delta t=\tau$ defined by

$$C_{\rm st}^{(n:m)}(\tau):=\langle\xi^n(t)\xi^m(t-\tau)\rangle_{\rm st} = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty}x^n y^m\,\mathcal{P}_{\rm st}^{\rm NBC}(x,t;y,t-\tau)dx\,dy. \tag{22}$$

For example, for $\gamma_1=0$, the autocorrelation $C_{\rm st}^{(2:2)}(\tau)$ reads

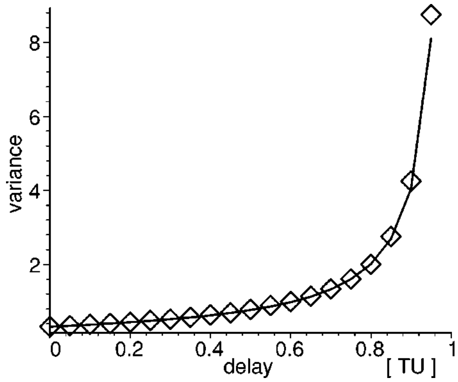

FIG. 1. Variances computed from the time-discrete stochastic delay equation (26) (diamonds) and from Eq. (15) (solid line) for different delays τ. A singularity occurs at the critical delay $\tau_c=1$.

$$C_{\rm st}^{(2:2)}(\tau;\gamma_1=0)=\langle \xi^2(t)\xi^2(t-\tau)\rangle_{\rm st}=\frac{1}{4a(\tau)\lambda(\tau)}+\frac{3\,b^2(\tau)}{4\lambda^2(\tau)} \tag{23}$$

$$=[\sigma^2(\tau)]^2+\frac{1}{2\gamma_2^2}. \tag{24}$$

Note that to obtain Eq. (24) from Eq. (23), we used $\sigma^2(\tau)=1/2\lambda(\tau)$ and Eq. (14).

The stationary solution of the stochastic process [Eq. (2)] given by Eqs. (9)–(11) and Eqs. (14) and (16) can also be used to describe the stationary solution of the original stochastic process [Eq. (1)]. To this end, we substitute the variables γ_1, γ_2, and τ by γ_1'/Q', γ_2'/Q', and $Q'\tau'$, which gives us

$$\lambda(\tau')=\frac{1}{Q'}\,\frac{\sqrt{\gamma_2'^2-\gamma_1'^2}\cdot[\gamma_1'+\gamma_2'\cos(\sqrt{\gamma_2'^2-\gamma_1'^2}\tau')]}{\gamma_2'\sin(\sqrt{\gamma_2'^2-\gamma_1'^2}\tau')+\sqrt{\gamma_2'^2-\gamma_1'^2}},$$

$$a(\tau')=\frac{\lambda(\tau')}{1-\left(\dfrac{Q'\lambda(\tau')-\gamma_1'}{\gamma_2'}\right)^2},\quad b(\tau')=\frac{Q'\lambda(\tau')-\gamma_1'}{\gamma_2'} \tag{25}$$

for $0\leqslant\tau'\sqrt{\gamma_2'^2-\gamma_1'^2}<\arccos(-\gamma_1'/\gamma_2')\leqslant\pi$.

B. Numerics

In line with the Euler method for ordinary Langevin equations [16,41,42], we discretized the SDDE (2) in terms of a time-discrete stochastic delay equation

$$\xi_{n+1}=\xi_n+\Delta(\gamma_1\xi_n+\gamma_2\xi_{n-m})+\sqrt{\Delta}w_n,\quad n\geqslant 0 \tag{26}$$

(see also Ref. [43] Sec. 5). Accordingly, time was measured in steps of Δ (i.e., $t=i\Delta$ and $\tau=m\Delta$) and the fluctuation force was approximated by the random numbers w_n. We used $\Delta=0.01$, and focused on the effect of the delay term, that is, we put $\gamma_1=0$ and $\gamma_2\neq0$. In detail, we used $\gamma_2=\pi/2$, which implies a critical delay $\tau_c=1$ [cf. our comment following Eq. (2) above]. Our simulation was based on an ensemble of $N=10\,000$ realizations of ξ_n. As an initial condition (the graph defined on $[-\tau,0]$) we used a series of random numbers selected from a Gaussian distribution with unit variance. The random numbers w_n were calculated by means of a Box-Muller algorithm. For each realization of ξ_n we iterated Eq. (26) $n_f=5000$ times, assuming that the set $\{\xi_{n_f}\}$ would reflect the stationary behavior of the ensemble. From the ensemble $\{\xi_{n_f}\}$ we calculated the mean $M_{0,\rm num}$, the variance $\sigma^2_{\rm num}$, and the shifted fourth and sixth moments [72] defined by $M_{4,\rm num}:=\langle[\xi_{n_f}-\langle\xi_{n_f}\rangle]^4\rangle$ and $M_{6,\rm num}:=\langle[\xi_{n_f}-\langle\xi_{n_f}\rangle]^6\rangle$. The diamonds in Figs. 1, 2, and 3 represent the numerical results for $\sigma^2_{\rm num}$, $M_{4,\rm num}$, and $M_{6,\rm num}$ for different delays.

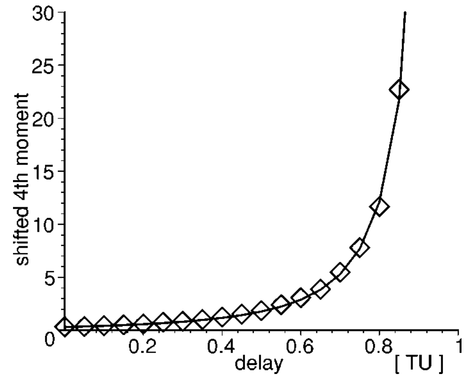

FIG. 2. Shifted fourth moments computed from the time-discrete stochastic delay equation (26) (diamonds) and from the Fokker-Planck approach solution (solid line) given by Eqs. (9) and (16) for different delays τ.

According to the Fokker-Planck approach (FPA), the stationary solution is a Gaussian distribution. Consequently, the shifted moments can be expressed in terms of the variance σ^2: $M_{4,\rm FPA}=3[\sigma^2]^2$ and $M_{6,\rm FPA}=15[\sigma^2]^3$, where σ^2 is described by Eq. (15). These analytical results are depicted as solid lines in Figs. 1 (σ^2), 2 ($M_{4,\rm FPA}$), and Fig. 3 ($M_{6,\rm FPA}$). By comparison, we realize that the numerical simulations of

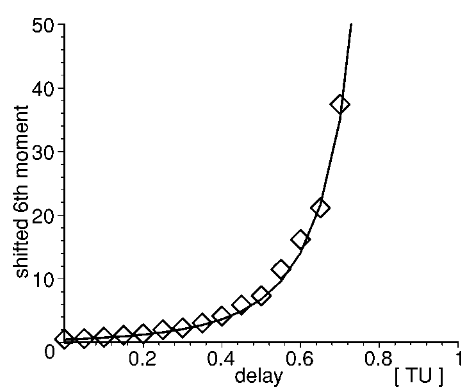

FIG. 3. Shifted sixth moments computed from the time-discrete stochastic delay equation (26) (diamonds) and from the Fokker-Planck approach solution (solid line) given by Eqs. (9) and (16) for different delays τ.

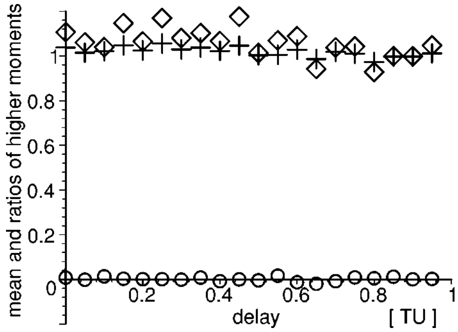

FIG. 4. Circles denote mean values obtained from the time-discrete stochastic delay equation (26) for different delays τ. Crosses and diamonds correspond to the ratios $M_{4,\mathrm{num}}/M_{4,\mathrm{FPA}}$ and $M_{6,\mathrm{num}}/M_{6,\mathrm{FPA}}$, respectively. See the text for details.

the delay Langevin equation (2) are in agreement with the Fokker-Planck solution [Eq. (9)] derived from Eq. (5). Fig. 4 shows the mean $M_{0,\mathrm{num}}$ of the set $\{\xi_{n_f}\}$ (circles) as well as the ratios $M_{4,\mathrm{num}}/M_{4,\mathrm{FPA}}$ (crosses) and $M_{6,\mathrm{num}}/M_{6,\mathrm{FPA}}$ (diamonds). Both ratios, $M_{4,\mathrm{num}}/M_{4,\mathrm{FPA}}$ and $M_{6,\mathrm{num}}/M_{6,\mathrm{FPA}}$, are close to unity, with $M_{6,\mathrm{num}}/M_{6,\mathrm{FPA}}$ having larger deviations from unity than $M_{4,\mathrm{num}}/M_{4,\mathrm{FPA}}$. Figure 5 shows the 3:1 autocorrelation [Eq. (21)] computed from the time-discrete stochastic delay equation (26) as $\langle(\xi_{n_f})^3\xi_{n_f-m}\rangle$ (diamonds) and from the analytical Fokker-Planck solution [Eq. (21)] (solid line). Again, analytical and numerical results were found to be in good agreement. The 1:1 autocorrelation $\langle\xi_{n_f}\xi_{n_f-m}\rangle$ was also computed and found to be approximately constant with $\langle\xi_{n_f}\xi_{n_f-m}\rangle\approx 0.31$ for all delays $\tau\in[0,1)$, which is in line with Eq. (8) for $\gamma_1=0$ and $\gamma_2=\pi/2$.

So far, our simulations verified the stationary probability density $\mathcal{P}_{\mathrm{st}}^{\mathrm{NBC}}(x)$ [see Eq. (9)], and the n:1 autocorrelations [Eq. (20)], which can be derived from $\mathcal{P}_{\mathrm{st}}^{\mathrm{NBC}}(x)$ via Eqs. (7) and (8), irrespective of the explicit structure of the joint probability density $\mathcal{P}_{\mathrm{st}}^{\mathrm{NBC}}(x,t;y,t-\tau)$ given by Eq. (11). In order to verify the explicit structure of $\mathcal{P}_{\mathrm{st}}^{\mathrm{NBC}}(x,t;y,t-\tau)$ and, in particular, the parameters $a(\tau)$ and $b(\tau)$ described by Eqs. (14) and (16), we studied the 2:2 autocorrelation $C_{\mathrm{st}}^{(2:2)}(\tau;\gamma_1=0)$, which involves the parameters $a(\tau)$ and

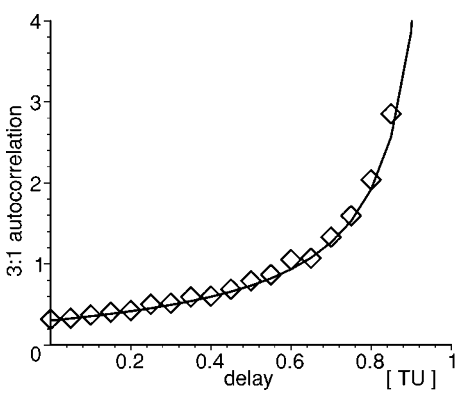

FIG. 5. Comparison of the 3:1 autocorrelation obtained from numerical simulations (diamonds), and from the Fokker-Planck approach solution (21) for different delays.

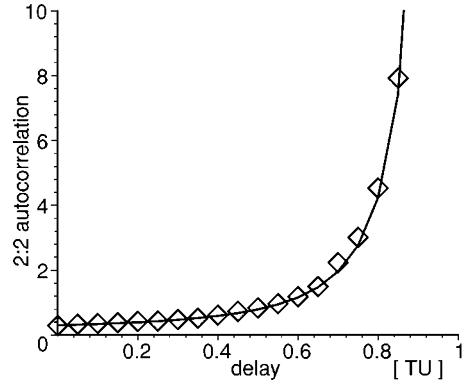

FIG. 6. Comparison of the 2:2 autocorrelation obtained from numerical simulations (diamonds) and from the Fokker-Planck approach solution (24) for different delays.

$b(\tau)$ [cf. Eq. (23)], and can only be determined by means of the explicit ansatz [Eq. (11)] for $\mathcal{P}_{\mathrm{st}}^{\mathrm{NBC}}(x,t;y,t-\tau)$ [cf. Eq. (22)]. In detail, we computed $C_{\mathrm{num}}^{(2:2)}:=\langle\xi_{n_f}^2\xi_{n_f-m}^2\rangle$ using our simulation scheme [Eq. (26)], and calculated $C_{\mathrm{FPA}}^{(2:2)}$ by means of Eqs. (15) and (24); see Fig. 6. Again, theoretical and numerical results were found to be in excellent agreement.

III. APPLICATIONS AND SPECIAL NONLINEAR CASES

A. Stochastic time lag model for population growth—weak nonlinearities and strong noise

In many cases, the evolution of the size of a population is determined by two contrasting effects. On the one hand, small populations typically grow exponentially (Malthusian law). On the other hand, when approaching critical population sizes growth rates of populations usually decrease (saturation effect) and population sizes converge to stable stationary values; see, e.g., Refs. [44,45]. A prominent model that can account for these observations is given by

$$\frac{d}{dt'}N(t')=kN(t')G(N(t'))\quad\text{for } t'\geqslant t_0', \tag{27}$$

and $N(t_0')=N_0>0$, where N denotes the population size, $k>0$ is the so-called intrinsic rate of increase, and $G(z)$ with $G(z^*)=0$ for a particular $z^*>0$ describes the self-regulation of the population dynamics leading to a saturation effect and a stable stationary population size $N_{\mathrm{st}}=z^*$ [44,46,47]. Two special cases are worth mentioning: the logistic model with $G(z):=(1-z/z^*)$ [44,45] and the Gompertz model with $G(z):=-\ln(z/z^*)$ [46–48]. They can be viewed as special cases of $G(z):=[1-(z/z^*)^{1-q}]/(1-q)$ for $q=0$ and $q\to 1$ [49]. Fluctuations of the population dynamics can be modeled in various ways. For example, it has been suggested to consider extensive (size-dependent) random forces which leads to

$$\frac{d}{dt'}N(t')=k\,N(t')G(N(t'))+\sqrt{Q'}\,N(t')\,\Gamma'(t'), \tag{28}$$

where $\Gamma'(t')$ denotes a Langevin force [46,47,50] or represents a Poisson process [48], and Q' corresponds to the strength of the fluctuations. In line with Sec. II, in this paper, $\Gamma'(t')$ is assumed to be a Langevin force. The multiplicative noise term can be interpreted, for example, as evolutionary disasters proportional to the population size N [48] or as a random contribution to the growth function G (i.e., $kG \to kG+\sqrt{Q'}\Gamma'$) [50]. Note that the stochastic process described by Eq. (28) is subjected to mixed boundary conditions, that is, we have a reflective boundary at the origin ($N=0$) and a natural boundary for $N\to\infty$. The evolution equation (28) suffers from the tacit assumption that the effective growth rate kG is determined by the instantaneous population size $N(t)$, that is, $kG=kG(N(t))$. In general, growth rates depend on the histories of populations which implies that we have to replace $kG(N(t'))$, for example, by $k\int_{-\infty}^{t'} N(a)s(t'-a)da$ [46,51] or by $k\int_{a_1}^{a_2} G(N(t'-a))s(a)da$ [47] with $a_2>a_1$, where $s(z)\geqslant 0$ weights the contributions of $N(t')$, and the integrals are often called Volterra integrals. When simplifying the Volterra integrals, we arrive at population dynamics models with constant time lags involving growth functions of the form $kG(N(t'-\tau'))$, where the delay τ' may be related to the so-called egg-to-adult time (or maturation or generation time) [44,47,52]. Inserting this assumption into Eq. (28) we obtain

$$\frac{d}{dt'}N(t')=kN(t')G(N(t'-\tau'))+\sqrt{Q'}N(t')\Gamma'(t'). \tag{29}$$

To study the effect of the delay length τ' on the population dynamics, we will use the Gompertz term because this allows us to use the result derived in Sec. II. Since other G functions, such as the function of the logistic model, are qualitatively similar to the Gompertz function, the findings obtained in the following may also carry over to other population dynamics models. For the Gompertz term, Eq. (29) reads

$$\frac{d}{dt'}N(t')=-kN(t')\ln\left(\frac{N(t'-\tau')}{z^*}\right)+\sqrt{Q'}N(t')\Gamma'(t'). \tag{30}$$

Following Refs. [47,48,50], we introduce the new variable $\xi'(t'):=\ln(N(t')/z^*)$ for $\xi'\in\mathbb{R}$, and transform Eq. (30) into

$$\frac{d}{dt'}\xi'(t')=-k\xi'(t'-\tau')+\sqrt{Q'}\Gamma'(t'). \tag{31}$$

Consequently, the stationary probability density $\mathcal{P}_{\rm st}(x)$ of the process ξ' exists for $k\tau'\in[0,\pi/2)$, and is given by Eqs. (9) and (25) with $\gamma_1'=0$ and $\gamma_2'=k$. Furthermore, let $\mathcal{W}_{\rm st}(N)$ denote the stationary probability density of the SDDE (30). Then, $\mathcal{W}_{\rm st}(N)$ can be derived from $\mathcal{P}_{\rm st}(x)$ by means of

$$\begin{aligned}\mathcal{W}_{\rm st}(N)dN=\mathcal{P}_{\rm st}(x)dx \Rightarrow \mathcal{W}_{\rm st}(N) &= \frac{1}{N}\mathcal{P}_{\rm st}\left(\ln\frac{N}{z^*}\right)\\ &= \frac{1}{N}\sqrt{\frac{\lambda(\tau')}{\pi}}\left[\frac{N}{z^*}\right]^{-\lambda(\tau')\ln(N/z^*)},\end{aligned} \tag{32}$$

with

$$\lambda(\tau')=\frac{k\cos(k\tau')}{Q'[1+\sin(k\tau')]}, \tag{33}$$

and $\lim_{N\to 0}\mathcal{W}_{\rm st}(N)=\lim_{N\to\infty}\mathcal{W}_{\rm st}(N)=0$ for $\lambda>0$ and $k\tau'\in[0,\pi/2)$. In particular, for $\tau'=0$ (i.e., for $\lambda=k/Q'$), Eq. (32) recovers the result obtained by Goel *et al.* (Ref. [47], 2.20a). We can now study the effect of τ' on the population dynamics. To this end, we consider the mean stationary population size

$$\begin{aligned}\langle N\rangle(\tau') &= \sqrt{\frac{\lambda(\tau')}{\pi}}\int_0^\infty\left[\frac{N}{z^*}\right]^{-\lambda(\tau')\ln(N/z^*)}dN\\ &= \sqrt{\frac{\lambda(\tau')}{\pi}}\int_0^\infty \exp\{-\lambda(\tau')[\ln(N/z^*)]^2\}dN.\end{aligned} \tag{34}$$

Differentiating $\langle N\rangle(\tau')$ with respect to τ', we obtain

$$\frac{d}{d\tau'}\langle N\rangle(\tau')=\frac{d\langle N\rangle(\lambda)}{d\lambda}\,\frac{d\lambda(\tau')}{d\tau'}, \tag{35}$$

$$\frac{d\langle N\rangle(\lambda)}{d\lambda}=-\left[\frac{\langle N\rangle}{2\lambda(\tau')}+\int_0^\infty N[\ln(N/z^*)]^2\mathcal{W}_{\rm st}(N)dN\right]<0, \tag{36}$$

$$\frac{d\lambda(\tau')}{d\tau'}=-\frac{k^2[1-\sin(k\tau')]}{Q'[1+\sin(k\tau')]^2}\tau'<0 \quad \text{for} \quad \tau'>0. \tag{37}$$

We can appreciate from Eq. (37) that $\lambda(\tau')$ is a monotonically decreasing function for $\tau'>0$, which is in agreement with our observation in Sec. II B that the variance $\sigma^2=1/2\lambda$ increases when the delay length is increased. From Eq. (35), it then follows that the mean population size $\langle N\rangle$ increases monotonically for $\tau'>0$. Figure 7 shows the probability density $\mathcal{W}_{\rm st}(N)$ for several delays τ'. We appreciate that an increase of the time delay τ' [which implies a decrease of the decay coefficient λ, cf. Eq. (37)] results in a shift of the positions of the peaks of the distributions $\mathcal{W}_{\rm st}(N)$ toward the origin. In addition, the tails of the distributions become more pronounced for larger delays; see Fig. 8. As a net effect, there is an increase of the mean value $\langle N\rangle$, cf. Eqs. (35)–(37).

In sum, the stochastic Gompertz model with delay has illustrated that we can take advantage of the stationary probability density derived in Sec. II in order to analyze nonlinear

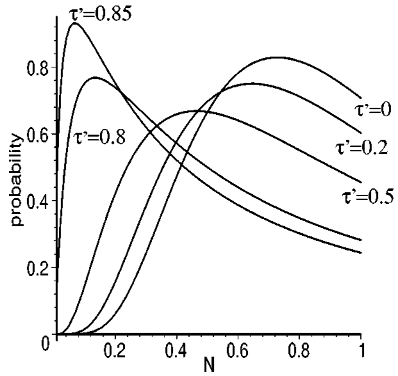

FIG. 7. Probability densities $\mathcal{W}_{st}(N)$ computed from Eq. (32) for several delays τ' and $k=\pi/2$, $Q'=1$ and $z^*=1$. From this follows a critical delay of $\tau_c'=1$. Population sizes N are depicted here in dimensionless units.

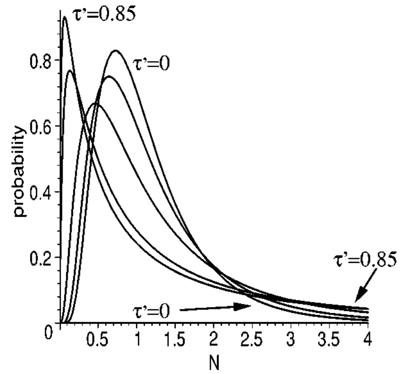

FIG. 8. Probability densities $\mathcal{W}_{st}(N)$ as in Fig. 7, but for $N \in [0,4]$.

SDDE's, provided that the nonlinearities are weak in the sense that we can transform the nonlinear equations into linear ones. In addition, we have observed an important effect of the delay on the mean population size, namely, the increase of the mean population size when the time delay is increased.

B. Pretransition variability of tracking movements with delayed feedback—strong nonlinearities and weak noise

The increase of time delays in systems with feedback control can destabilize system states. In several instances, transitions from a stable fixed point behavior to an oscillatory behavior can be observed when the delay time or the gain of delay feedback loops is increased; for example, in semiconductor laser with optical injection [53], in population dynamics [44], in the human pupil light reflex [3], and in tracking movements [8]. In general, the reduction of the stability of a spatiotemporal pattern exhibited by a system due to changes of system parameters can be studied both from deterministic and stochastic points of view. In the former case, destabilization is revealed by qualitative transitions between characteristic spatiotemporal patterns as mentioned above [54–57]. In the latter case, the reduction of the stability of a particular spatio-temporal pattern is often accompanied by an increase in pattern variability in subcritical or pretransition parameter regimes [18,58–63]. In this section, we will discuss the pretransition variability of a system that is known to exhibit delay induced transitions from fixed point behavior to oscillatory behavior: the human motor control system involved in unimanual tracking tasks with delayed visual feedback. To this end, we will analyze a theoretical model [7], which was found to be in good qualitative agreement with experimental findings [8].

In unimanual tracking tasks, subjects look at a screen and watch an oscillating target signal. They can move their arm or hand, and in doing so they can produce a second signal on the screen—a manual response signal. The displacement of the manual response signal corresponds to the displacement of the limb that has to be moved. The task is to match the response signal with the target signal. The manual response signal is displayed on the screen with a particular fixed delay $\tau_{\rm ext}'$. The tracking movement can then be studied for various oscillation frequencies Ω of the target signal and for different delays $\tau_{\rm ext}'$.

Tass *et al.* developed a deterministic model which describes the evolution of the relative phase ϕ between the target signal and the limb movement [7]. According to this model, the change of the relative phase ϕ per unit time depends on two terms

$$\frac{d}{dt'}\phi(t') = \underbrace{-\alpha \sin\left(\phi(t') - \frac{\Omega\tau'}{2}\right)}_{I} \underbrace{-\beta \sin\left(\phi(t'-\tau') + \frac{\Omega\tau'}{2}\right)}_{II} \tag{38}$$

with $\alpha > 0$, $\beta > 0$, and $\tau' \approx \tau_{\rm ext}'$ (also see below). The nonlinearities occurring in Eq. (38) are consistent with neurophysiological findings. First, in the study of human eye tracking it was argued that human pursuit systems are more than linear response systems, and that nonlinearities contribute essentially to the dynamics of these systems [64]. In a similar vein, observations of eye movement trajectories indicate that asymmetric force-velocity characteristics of eye muscles play a crucial role in the control of eye movements. Such asymmetric characteristics, in turn, can hardly be explained in terms of linear models [65]. Furthermore, to account for experimentally observed asymmetries of velocity profiles of hand movements, Bullock and Grossberg introduced a nonlinear element in their neural model for the control of goaldirected movements: a gain signal that interacts in a multiplicative fashion with another neural signal [66]. As shown in Ref. [7], term I describes the proprioceptive control of the tracking movement, and affects the change of the relative phase ϕ instantaneously, whereas term II describes the effect of the visual control. In the time argument of this expression we find the delay τ' that was originally proposed to be equal to the artificial delay τ'_{ext}. However, the model by Tass *et al.* does not incorporate intrinsic delays of the visual and proprioceptive system, which are in the order of 60 ms for eye movements [64] and in the range of 30–90 ms for limb movements [67,68]. Since in the tracking experiment the artificially introduced delay τ'_{ext} was gradually increased from $\tau'_{\mathrm{ext}}=0$ in steps between 25 and 50 ms [8], we need to take possible interactions between intrinsic delays and the artificial delay into account. To this end, we introduce the effective delays $\tau'_{\mathrm{vis,tot}}$ and $\tau'_{\mathrm{prop,tot}}$ that describe the total delays of the proprioceptive and visual systems, respectively (for an analogous situation, see Ref. [3]). Accordingly, we modify Eq. (38), and obtain

$$\frac{d}{dt'}\phi(t') = -\alpha \sin\left(\phi(t') - \frac{\Omega \tau'_{\mathrm{prop,tot}}}{2}\right) - \beta \sin\left(\phi(t'-\tau'_{\mathrm{vis,tot}}) + \frac{\Omega \tau'_{\mathrm{vis,tot}}}{2}\right). \quad (39)$$

We assume that $\tau'_{\mathrm{vis,tot}}$ and $\tau'_{\mathrm{prop,tot}}$ are positively correlated with the artificially introduced delay τ'_{ext} (i.e., $d\tau'_{\mathrm{vis,tot}}/d\tau'_{\mathrm{ext}} > 0$ and $d\tau'_{\mathrm{prop,tot}}/d\tau'_{\mathrm{ext}} > 0$). Since we aim at a discussion of motor variability, we extend the deterministic model with a white noise force $\Gamma(t')$ with a fluctuation strength Q'. Thus we obtain

$$\frac{d}{dt'}\phi(t') = -\alpha \sin\left(\phi(t') - \frac{\Omega \tau'_{\mathrm{prop,tot}}}{2}\right) - \beta \sin\left(\phi(t'-\tau'_{\mathrm{vis,tot}}) + \frac{\Omega \tau'_{\mathrm{vis,tot}}}{2}\right) + \sqrt{Q'}\,\Gamma(t'). \quad (40)$$

Note that more elaborate discussions involving colored noise forces may be carried out by extending the dimensionality of the problem [3,35,41]. In order to obtain some fundamental insights into the effect of the artificial delay τ'_{ext} on the variability of the phase dynamics [Eq. (40)], we confine ourselves to the discussion of the stationary case for weak fluctuation forces. More precisely, as suggested in the deterministic case with delay [3,46,47,69], in the stochastic case without delay (Ref. [41], Sec. 5.10), and in the general stochastic case with delay [35], we consider linear SDDE's as approximations of nonlinear SDDE's. Consequently, we calculate first from Eq. (40) the stationary solution ϕ_{st} for $Q'=0$, which satisfies

$$\alpha \sin\left(\phi_{\mathrm{st}} - \frac{\Omega \tau'_{\mathrm{prop,tot}}}{2}\right) = -\beta \sin\left(\phi_{\mathrm{st}} + \frac{\Omega \tau'_{\mathrm{vis,tot}}}{2}\right) \quad (41)$$

and is explicitly given by

$$\phi_{\mathrm{st}} = \arctan\left\{\frac{\alpha \sin(\Omega \tau'_{\mathrm{prop,tot}}/2) - \beta \sin(\Omega \tau'_{\mathrm{vis,tot}}/2)}{\alpha \cos(\Omega \tau'_{\mathrm{prop,tot}}/2) + \beta \cos(\Omega \tau'_{\mathrm{vis,tot}}/2)}\right\}. \quad (42)$$

Next we linearize Eq. (40) with respect to ϕ_{st}, and obtain

$$\frac{d}{dt'}\xi(t') = -\gamma'_1 \xi(t') - \gamma'_2 \xi(t'-\tau'_{\mathrm{vis,tot}}) + \sqrt{Q'}\,\Gamma(t'), \quad (43)$$

with

$$\gamma'_1 := \alpha \cos\left(\phi_{\mathrm{st}} - \frac{\Omega \tau'_{\mathrm{prop,tot}}}{2}\right) \quad \text{and} \quad \gamma'_2 := \beta \cos\left(\phi_{\mathrm{st}} + \frac{\Omega \tau'_{\mathrm{vis,tot}}}{2}\right) \quad (44)$$

and $\xi(t') := \phi(t') - \phi_{\mathrm{st}}$. Furthermore, from Eqs. (41) and (44), it follows that ${\gamma'_2}^2 - {\gamma'_1}^2 = \beta^2 - \alpha^2$. In Sec. II we have argued that the inequality $\gamma'_2 > \gamma'_1 \geqslant 0$ should hold. Consequently, here we assume $\beta > \alpha \Rightarrow \gamma'_2 > 0 \wedge \gamma'_2 > \gamma'_1$ and $2\phi_{\mathrm{st}} - \Omega \tau'_{\mathrm{prop,tot}} \in [-\pi/2, \pi/2] \Rightarrow \gamma'_1 > 0$. The stationary probability density of $\xi(t')$ described by the linearized equation (43) is given by Eq. (9) [73]. The variance σ^2 of $\xi(t')$ can then be derived from Eq. (25), and reads

$$\frac{1}{2\sigma^2} = \lambda = \frac{C}{Q'} \frac{[\sqrt{{\gamma'_2}^2 - C^2} + \gamma'_2 \cos(C\tau'_{\mathrm{vis,tot}})]}{\gamma'_2 \sin(C\tau'_{\mathrm{vis,tot}}) + C}, \qquad C := \sqrt{\beta^2 - \alpha^2}. \quad (45)$$

The decay coefficient λ varies with τ'_{ext} according to

$$\frac{d}{d\tau'_{\mathrm{ext}}}\lambda = \underbrace{-\frac{{\gamma'_2}^2 C^2 [1 + \sin(C\tau'_{\mathrm{vis,tot}} + \theta)]}{Q'[\gamma'_2 \sin(C\tau'_{\mathrm{vis,tot}}) + C]^2} \frac{d\tau'_{\mathrm{vis,tot}}}{d\tau'_{\mathrm{ext}}}}_{A<0} + \underbrace{\frac{d\lambda}{d\gamma'_2} \frac{d\gamma'_2(\tau'_{\mathrm{prop,tot}}, \tau'_{\mathrm{vis,tot}})}{d\tau'_{\mathrm{ext}}}}_{B} \quad (46)$$

with $\tan\theta := \sqrt{[\gamma'_2/C]^2 - 1}$. On account of the impact of the B term, the variance might increase or decrease when τ'_{ext} is increased. However, if the B term can be neglected with respect to the A term, then the increase of the variance with increasing delay is guaranteed; that is, we obtain

$$\frac{d}{d\tau'_{\mathrm{ext}}}\lambda<0 \quad \Rightarrow \quad \frac{d}{d\tau'_{\mathrm{ext}}}\sigma^2>0. \tag{47}$$

In particular, for small delays and target frequencies (i.e., $\Omega\tau'_{\mathrm{prop,tot}}\approx 0$ and $\Omega\tau'_{\mathrm{vis,tot}}\approx 0$) we find $\phi_{\mathrm{st}}\approx 0$, $\gamma'_1\approx\alpha$, and $\gamma'_2\approx\beta$. Then, it follows from Eq. (44) that

$$\frac{d\gamma'_2(\tau'_{\mathrm{prop,tot}},\tau'_{\mathrm{vis,tot}})}{d\tau'_{\mathrm{ext}}}=-\beta\underbrace{\sin\left(\phi_{\mathrm{st}}+\frac{\Omega\tau'_{\mathrm{vis,tot}}}{2}\right)}_{\approx 0}\left[\frac{d\phi_{\mathrm{st}}(\tau'_{\mathrm{prop,tot}},\tau'_{\mathrm{vis,tot}})}{d\tau'_{\mathrm{ext}}}+\frac{d\tau'_{\mathrm{vis,tot}}}{d\tau'_{\mathrm{ext}}}\right]\approx 0. \tag{48}$$

Consequently, for small delays and low tracking frequencies, the B term can be neglected. In this case, Eq. (46) reduces to

$$\frac{d}{d\tau'_{\mathrm{ext}}}\lambda=-\frac{\beta^2C^2[1+\sin(C\tau'_{\mathrm{vis,tot}}+\theta_0)]}{Q'[\beta\sin(C\tau'_{\mathrm{vis,tot}})+C]^2}\,\frac{d\tau'_{\mathrm{vis,tot}}}{d\tau'_{\mathrm{ext}}}<0, \tag{49}$$

with $\tan\theta_0:=\alpha/\sqrt{\beta^2-\alpha^2}$ implying that, with increasing delay τ_{ext}, the decay coefficient λ decreases and, consequently, the variance σ^2 increases.

In sum, we demonstrated explicitly the application of the concepts of delay Fokker-Planck equations to linearized SDDE's. As an example, we used a SDDE that describes unimanual tracking movements in terms of the relative phase between the target signal and the limb movement. In line with the deterministic model that shows that the stability of fixed point behavior is lost when the artificially introduced time delay is increased beyond a critical value, we found particular conditions in which the variance of the relative phase increases with increasing time delay. However, our analysis also showed that another scenario is possible: variance might decrease with increasing time delay [cf. the B term in Eq. (46)].

IV. DISCUSSION

We showed that stationary probability densities for linear SDDE's can be derived by means of the corresponding delay Fokker-Planck equations. The crucial step was to find a stationary joint probability density ${}^{a,b,\lambda}\mathcal{P}^{\mathrm{NBC}}_{\mathrm{st}}(x,t;y,t-\tau)$ depending on a set of parameters (a,b,λ) which (i) satisfies the self-consistent condition $\int {}^{a,b,\lambda}\mathcal{P}^{\mathrm{NBC}}_{\mathrm{st}}dx=h_1(y)$, $\int {}^{a,b,\lambda}\mathcal{P}^{\mathrm{NBC}}_{\mathrm{st}}dy=h_2(x)\Rightarrow h_1(z)=h_2(z)=h(z)$, (ii) is consistent with the stationary solution [i.e., $h(z)={}^{a,b,\lambda}\mathcal{P}^{\mathrm{NBC}}_{\mathrm{st}}(z)$], and (iii) solves the delay Fokker-Planck equation. On the basis of these constraints, we were able to determine all the parameters but one. The decay coefficient λ was obtained from a detailed analysis of the corresponding linear SDDE. In particular, in this analysis an exact expression for the autocorrelation $K^{(1)}_{\mathrm{st}}(\Delta t)$ for arbitrary time shifts Δt was derived, and λ was computed as $\lambda=1/2K^{(1)}_{\mathrm{st}}(0)$ [36]. It is obvious that a delay Fokker-Planck equation of the form of Eq. (3) does not provide sufficient information for a calculation of $K^{(1)}_{\mathrm{st}}(\Delta t)$ for arbitrary Δt. Therefore, future studies focusing on SDDE-independent derivations of stationary solutions of linear delay Fokker-Planck equations need to follow approaches different from the SDDE approach.

As already stated in Sec. I, in general, stationary probability densities of nonlinear stochastic differential equations can only be derived indirectly using the theory of Fokker-Planck equations. Consequently, delay Fokker-Planck equations are the necessary tool for obtaining stationary distributions of nonlinear SDDE's. In addition, following van Kampen [70], the derivation of evolution equations of stochastic quantities in two complementary ways (using SDDEs and delay Fokker-Planck equations) can help us to uncover further details of the stochastic processes under study. For example, for $n\geqslant 1$, from the SDDE (2) it follows that

$$\frac{d}{dt}\langle x^n\rangle=-n\gamma_1\langle x^n\rangle-n\gamma_2\langle x^{n-1}(t)x(t-\tau)\rangle +n\langle x^{n-1}(t)\Gamma(t)\rangle, \tag{50}$$

whereas from the delay Fokker-Planck equation (3) we obtain

$$\frac{d}{dt}\langle x^n\rangle=-n\gamma_1\langle x^n\rangle-n\gamma_2\langle x^{n-1}(t)x(t-\tau)\rangle +n(n-1)\langle x^{n-2}(t)\rangle. \tag{51}$$

By virtue of Eqs. (50) and (51), we can then calculate the transient cross-correlations between the stochastic process $\xi(t)$ given by Eq. (2) and the Langevin force Γ, and find

$$\langle x^m(t)\Gamma(t)\rangle=m\langle x^{m-1}(t)\rangle,\quad m\geqslant 1. \tag{52}$$

In particular, we have $\langle x(t)\Gamma(t)\rangle=1$ and, in the stationary case, $\langle x^2(t)\Gamma(t)\rangle_{\mathrm{st}}=0$. Relation (52) agrees with the relation between cross-correlations $\langle x^m(t)\Gamma(t)\rangle$ and moments $\langle x^m(t)\rangle$ of an Ornstein-Uhlenbeck process without delay. Of course, the values of the moments $\langle x^m(t)\rangle$ and cross-correlations $\langle x^m(t)\Gamma(t)\rangle$ will differ. Consequently, in the linear case, the correlations between the stochastic process $\xi(t)$ and its noise source $\Gamma(t)$ can be expressed in terms of higher moments of the process $\xi(t)$—irrespective of the delay τ.

This result can be immediately generalized to the nonlinear case. To this end, let us consider the nonlinear SDDE,

$$\frac{d}{dt}\xi(t)=g_1[\xi(t)]+g_2[\xi(t-\tau)]+\Gamma(t) \tag{53}$$

and the corresponding delay Fokker-Planck equation [37,38],

$$\frac{\partial}{\partial t}\mathcal{P}(x,t)=-\frac{\partial}{\partial x}g_1(x)\mathcal{P}(x,t)-\frac{\partial}{\partial x}\mathcal{P}(x,t)\times\int_{-\infty}^{\infty}g_2(y)\mathcal{P}(y,t-\tau|x,t)dy+\frac{1}{2}\frac{\partial^2}{\partial x^2}\mathcal{P}(x,t), \tag{54}$$

with natural boundary conditions; cf. Sec. II. Computing the evolution equations for $\langle x^n\rangle$ from Eqs. (53) and (54), we obtain

$$\begin{aligned}\frac{d}{dt}\langle x^n\rangle&=n\langle x^{n-1}g_1(x)\rangle+n\langle x^{n-1}(t)g_2(x(t-\tau))\rangle\\&\quad+n\langle x^{n-1}(t)\Gamma(t)\rangle,\\\frac{d}{dt}\langle x^n\rangle&=n\langle x^{n-1}g_1(x)\rangle+n\langle x^{n-1}(t)g_2(x(t-\tau))\rangle\\&\quad+n(n-1)\langle x^{n-2}(t)\rangle\end{aligned} \tag{55}$$

which again lead to Eq. (52). In sum, the theory of delay Fokker-Planck equations can uncover properties of time-continuous stochastic processes with delays that cannot be addressed by means of SDDE's alone.

In addition, we have shown that in special cases nonlinear SDDE's can be transformed into linear SDDE's, so that exact stationary probability densities for the nonlinear case can be derived. In Sec. III A, we illustrated this procedure with the Gompertz population model. We showed that an increase of the time delay or maturation time results in an increase of the mean population size. This result does not come as a surprise when we keep in mind that the stationary probability $\mathcal{W}_{\rm st}(N)$ of the population dynamics and the stationary probability density $\mathcal{P}_{\rm st}(x)$ of the linear SDDE (1) with $\gamma_1=0$ are related by a transformation which maps the real line ($x\in\mathbb{R}$) onto the positive half line ($N\in[0,\infty)$). The monotonic increase of the variance of the process defined on $\mathbb{R}$ [cf. Eq. (33)] then corresponds to a monotonic increase of the mean value of the process defined on the interval $[0,\infty)$. In view of this consideration and on account of the fact that the Gompertz growth function agrees qualitatively with many other growth functions and belongs to a class of simple functions (namely, monotonically decreasing functions), we expect that a similar effect of the delay on the mean population size can also be found in other population models.

Finally, we studied human motor variability during unimanual tracking with delayed feedback on the basis of a theoretical model proposed by Tass *et al.* [7]. Among other indicators such as relaxation time, performance variability is an important indicator for the stability of a movement pattern. In recognition of the fact that the increase of time delays in feedback loops can result in a breakdown of behavioral patterns and the emergence of interesting novel behavioral patterns, we expected to observe a positive correlation between variability and delay length, that is, a negative correlation between pattern stability and time delay. We confirmed this hypothesis by identifying particular model constraints for which an increase of the time delay yields an increase of variability. To this end, we examined a linearized SDDE. According to this equation, the change of variability is determined by two terms; cf. Eq. (46). The first term (the *A* term) describes change of variability due to an increase of the effective visual delay when the coefficients of the linearized model are fixed (i.e., $\gamma_2'^1\approx$const and $\gamma_2'^2\approx$const). This term results in a decrease of the decay coefficient λ, that is, in an increase of the variability. The second term (the *B* term) describes the impact of the shift of the coefficients of the linearized model on the variability. The sign of this term is likely to depend on the model parameter values. Therefore, there might be a reduction or an increase of variability due to the impact of this latter term. This example shows us that the concepts of the theory of ordinary stochastic processes without delay cannot necessarily be adopted in a one-to-one fashion for stochastic processes with delays. As is well known from the theory of deterministic delay equations, systems with delays can exhibit a variety of striking phenomena that are absent in systems without delays.

ACKNOWLEDGMENTS

We are grateful to Andreas Daffertshofer for sharing his original ideas on stochastic delay equations with us, as well as his intuitions regarding the relevance of their application to human motor control.

APPENDIX A: DERIVATION OF EQ. (12)

Inserting Eq. (9) in the right hand side ($\mathcal{R}$) of Eq. (7) gives us

$$\begin{aligned}\mathcal{R}&=-\gamma_1 x\mathcal{P}_{\rm st}^{\rm NBC}(x)-\frac{1}{2}\frac{\partial}{\partial x}\mathcal{P}_{\rm st}^{\rm NBC}(x)\\&=(\lambda-\gamma_1)\sqrt{\frac{\lambda}{\pi}}x\exp\{-\lambda x^2\}.\end{aligned} \tag{A1}$$

Substituting Eq. (11) in the left hand side ($\mathcal{L}$) of Eq. (7), we obtain

$$\mathcal{L}=\frac{\gamma_2}{\pi}\sqrt{\lambda a}\int_{-\infty}^{\infty}y\exp\{-a[x-by]^2-\lambda y^2\}dy. \tag{A2}$$

Using the identity

$$a[x-by]^2+\lambda y^2 = \left[a-\frac{a^2b^2}{ab^2+\lambda}\right]x^2+[ab^2+\lambda]\left[y-x\frac{ab}{ab^2+\lambda}\right]^2 = \frac{a\lambda}{ab^2+\lambda}x^2+[ab^2+\lambda]\left[y-x\frac{ab}{ab^2+\lambda}\right]^2, \quad \text{(A3)}$$

we find

$$\mathcal{L}=\frac{\gamma_2}{\pi}\sqrt{\lambda a}\exp\left\{-\frac{a\lambda}{ab^2+\lambda}x^2\right\} \times\int_{-\infty}^{\infty} y\exp\left\{-[ab^2+\lambda]\left[y-x\frac{ab}{ab^2+\lambda}\right]^2\right\}dy$$

$$\mathcal{L}=\frac{\gamma_2}{\pi}\sqrt{\lambda a}\exp\left\{-\frac{a\lambda}{ab^2+\lambda}x^2\right\} \times\int_{-\infty}^{\infty} y\exp\left\{-[ab^2+\lambda]\left[y-x\frac{ab}{ab^2+\lambda}\right]^2\right\}dy = \frac{\gamma_2}{\pi}\sqrt{\lambda a}\sqrt{\frac{\pi}{ab^2+\lambda}}x\frac{ab}{ab^2+\lambda}\exp\left\{-\frac{a\lambda}{ab^2+\lambda}x^2\right\} = \gamma_2\sqrt{\frac{\lambda}{\pi}}\frac{a^{3/2}b}{[ab^2+\lambda]^{3/2}}x\exp\left\{-\frac{a\lambda}{ab^2+\lambda}x^2\right\}. \quad \text{(A4)}$$

Finally, we divide Eqs. (A1) and (A4) by $\sqrt{\lambda/\pi}$, and thus obtain Eq. (12).

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[71] They studied the SDDE $\dot{\xi}(t)=\tilde{b}\xi(t-\tau)+\Gamma(t)$ [see Eq. (2.1a) in Ref. [36]], and found $K_{\mathrm{st}}(\tau)=-1/(2\tilde{b})$ [see Eq. (2.24) in Ref. [36]].
[72] We also calculated nonshifted fourth and sixth moments. The results were almost the same. Shifted moments, however, are more suitable to test the Gaussian shape of a distribution because they are insensitive to shifts of distributions like $\mathcal{P}(x)\to\mathcal{P}(x+c)$.
[73] Recall that we discuss the stationary case in the weak noise limit. Therefore, we can replace the periodic boundary conditions by natural boundary conditions.